Winter Forages and Diets of Elk in Old-Growth and Regenerating Coniferous Forests in Western Washington

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ABSTRACT.—Biomass of available elk (*Cervus elaphus*) forages was monitored throughout a winter cycle in an age sequence of 1–200+ yr-old Douglas-fir (*Pseudotsuga menziesii*)-western hemlock (*Tsuga heterophylla*) forests in the Cascade Mountains. Additionally, fecal pellets of elk were collected from old-growth and 1–35 yr-old regenerating forests, from which we estimated plant species composition, dry matter digestibility and crude protein content of the diets. We tested hypotheses that plant species composition of feces and nutritional indices of diets did not differ between those endpoints of the forest successional continuum. Trends in available forages following clear-cut logging were related to stand-age, topographic landform, season and snow accumulation. Elk feces contained mainly deciduous shrubs and herbaceous forages during November, conifers and evergreen shrubs during midwinter when snow largely covered herbaceous forages, and herbaceous forages during early spring regrowth. Elk feces from 1–35 yr-old regenerating forests contained more herbaceous forage overall during winter than did feces from elk in old growth (P ≤ 0.02). Consequently, we observed greater indices of dietary crude protein and dry-matter digestibility during winter in a 1–35 yr-old than in an old-growth forest ecosystem (P ≤ 0.05). Implications for elk populations and forest management are discussed.

INTRODUCTION

Elk (*Cervus elaphus*) are important components of montane and subalpine ecosystems throughout the northwestern United States, as well as important big game animals. Although elk populations have expanded throughout the region in recent decades, large-scale conversion of uneven-aged, old-growth forests to even-aged, regenerating forests following timber harvesting has raised concern that depletion of old-growth forests could affect these populations adversely (Raedeke and Lehmkuhl, 1985). Because carrying capacity of habitat and reproduction rates of Roosevelt elk (*C. e. roosevelti*) are widely considered to be limited by forage quality in the Pacific Northwest (Trainer, 1971; Starkey *et al.*, 1982; Leslie *et al.*, 1984), it is important to understand influences of forest harvesting on forages and dietary characteristics of elk.

Traditionally, mature western hemlock and Douglas-fir forests in the Pacific Northwest were considered poor foraging areas for elk and deer (*Odocoileus hemionus columbianus*) in comparison to early stages of forest regeneration following fire and timber harvesting (Cowan, 1945; Einarsen, 1946; Harper, 1985). Forage values of old growth, however, may have been underestimated relative to early seral stages of succession (Schoen *et al.*, 1981). Measurable benefits of old-growth forests include greater standing crop biomass of forage (Bunnell and Jones, 1984), reduced accumulation of snow, greater availability of forage (Harestad *et al.*, 1982), greater nutritive quality of shrubs (Van Horne *et al.*, 1988; Happe *et al.*, 1990), and greater availability of arboreal lichens and litterfall in old-growth than in immature

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forests (Stevenson and Rochelle, 1984). Furthermore, extensive harvest of old-growth forests may increase the proportion of mid-seral successional stages in a landscape and reduce forage values averaged throughout a forest harvesting rotation (Schoen *et al.*, 1981; Wallmo and Schoen, 1980). Although previous studies have described post-logging successional patterns of vegetation in Pacific Northwest forests (Irwin and Peek, 1979; Alaback, 1982; Hanley, 1984), most studies did not focus specifically on those forages available to large herbivores during winter. We are not aware of any previous studies that compared composition and quality of elk diets among areas dominated by different stages of forest succession.

The objectives of this study were to monitor trends in winter forage availability in an age-sequence of Douglas fir-western hemlock forests and to compare indices of dietary composition of elk in old-growth vs. 1–35 yr-old regenerating forests. We tested hypotheses that indices of diet composition, dry-matter digestibility, and crude protein content of elk diets did not differ between young, regenerating stands and old-growth forests.

STUDY AREAS

Forage availability and dietary characteristics of elk were investigated in two study areas of the White River drainage within and adjacent to Mount Rainier National Park, Washington. Study areas were defined by winter home ranges of two herds of elk that summer within Mount Rainier National Park (Cooper, 1987). The study area within the park (11.5 km²) consisted of alluvial wash communities (5.2%), riparian red alder (*Alnus rubra*) communities (1.5%) and old-growth Douglas-fir, western hemlock, and Pacific silver fir (*Abies amabilis*) forests (93.3%) (Cooper, 1987). Characteristic understory species included Oregongrape (*Berberis nervosa*), huckleberry (*Vaccinium* spp.), salal (*Gaultheria shallon*), trailing twinflower (*Linnaea borealis*), foamflower (*Tiarella* spp.) and vine maple (*Acer circinatum*) in old-growth forests, and devil's club (*Oplopanax horridum*), salmonberry (*Rubus spectabilis*), wildrye (*Elymus* sp.), bromegrass (*Bromus* sp.), foamflower, bedstraw (*Galium* sp.), and western spring beauty (*Montia sibirica*) in riparian alder communities.

A second study area (19.1 km²), 12 km downriver from the former, consisted of a mosaic of 0–20 yr-old (18%) and 21–35 yr-old (80%) regenerating second-growth forests managed by Weyerhaeuser Company, U.S. Forest Service and Washington Department of Natural Resources. Regenerating stands were dominated by even-aged red alder on moist bottomland sites (20%) and by Douglas fir on more xeric uplands (78%). Characteristic understory species in 21–35 yr-old Douglas fir included salal, Oregongrape and veronica (*Veronica officionale*), whereas younger Douglas fir plantations contained a variety of grasses, shrubs and forbs. Understories of seral red alder communities were dominated by wildrye, bromegrass, bedstraw, western spring beauty and water parsley (*Oenanthe sarmentosa*). Common shrubs included vine maple, salmonberry and trailing blackberry (*Rubus ursinus*). Elevations of the study areas ranged from 700–900 m in Mount Rainier National Park and 550–675 m in regenerating commercial forests downriver.

Elk populations in the White River drainage stem from native populations of Roosevelt elk supplemented with Rocky Mountain elk (*Cervus elaphus nelsoni*) transplanted to the surrounding region between 1912–1933 (Bradley, 1982). Wintering densities of elk in the study areas are not known; however, elk populations increased between 1974–1984 on adjoining summer ranges within the park (Cooper, 1987).

Although there were no weather stations operating during the study, annual precipitation in the White River averaged 152 cm from 1939–1980 at Greenwater, Washington, 2 km N of the commercially managed study area (NOAA, 1980). Monthly maximum accumu-

lations of snow during that interval averaged 7 cm (range = 0–30 cm), 50 cm (range = 0–137 cm) and 30 cm (range = 0–104 cm) in November, January and March, respectively (NOAA, 1980). Snowfall was below average during our study, occurring only sporadically and persisting for only 2–3 wk during January. Accumulations averaged 25 cm under open canopies and 14 cm in old-growth forests near Greenwater; snowpack averaged 5 cm deeper upriver within Mount Rainier National Park (K. Jenkins, unpubl. data). Study areas were snow-free during the remainder of the study.

METHODS

Forage availability.—Initial reconnaissance of the study areas suggested that vegetational patterns in the commercial forest study area were controlled principally by stand age (time elapsed since clear-cut logging), topographic position and forest regeneration practices (principally pre-commercial thinning of regenerating forests). As a basis for sampling forage availability trends in the commercial forest, stands of uniform vegetation were mapped on low-level 1:10,000-scale aerial photographs, and were aged using forest harvesting records provided by local land management agencies. Following ground reconnaissance, each stand was classed as mesic or xeric on the basis of topographic position: mesic stands were located in poorly-drained bottomlands, whereas xeric stands were situated on well-drained alluvial terraces. Additionally, regenerating stands were described as pre-commercially thinned if they had been thinned within 5 yr before the study.

Biomass of available forages was estimated between 7 October–15 November 1986 in 67 stands of 11 plant communities, characterized by combinations of stand age, soil moisture and management history (Table 1). Sampling was apportioned among communities based roughly on relative proportions of communities within the commercial forest. Stands of most communities sampled were selected randomly from the commercial forest study area. Old-growth (>200 yr-old) forests were scarce, however, so those communities were sampled from within Mount Rainier National Park and Federation Forest State Park (10 km N of the commercial forest study area).

Biomass of available forages was estimated based on measurements of canopy cover or density of current year's twigs within 10, 1 × 1-m quadrats distributed systematically along a randomly placed 90-m transect in each sample stand. Available forage was defined as plant species that comprised at least 1% of any autumn-spring diet of elk reported in the Pacific Northwest (Jenkins and Starkey, 1991), and as phytomass less than 225 cm aboveground, the observed maximum reach of a browsing elk. Canopy cover and heights of graminoids, forbs, low evergreen shrubs and fallen green leaves were estimated within each quadrat as a means of subsequently estimating biomass of available forages. Canopy cover was estimated to the nearest 5% using a sampling frame gridded in 5, 10 and 25% increments for reference. We also counted all current year's twigs of deciduous shrubs and conifers, as well as fronds of ferns below 225 cm in each quadrat.

Biomass of graminoids, forbs and low evergreen shrubs was estimated from canopy cover using weight-cover-height regression equations developed on the study area in November 1986, concurrent with vegetation sampling (Jenkins and Starkey, 1990). Regression equations were developed for each forage species by estimating canopy cover and height within 12, 0.25-m² quadrats and then clipping, drying and weighing the clipped material. Biomass of deciduous shrubs, conifers and ferns was computed as the product of twig counts obtained within quadrats and average oven-dried weight per twig. Average oven-dried weights of twigs were determined from a minimum of 50 randomly sampled twigs or fronds of each species collected concurrent with vegetation sampling (Jenkins and Starkey, 1990).

TABLE 1.—Mean standing crop biomass (g dry-matter/m²) of forage classes available to elk (<225 cm in height) in mesic and xeric plant communities and seral stages, 15 October–7 November 1986

Plant community/Seral stage	No. stands sampled (n)	Percent- age of study area	Standing crop biomass												
			Conifers		Deciduous shrubs		Evergreen shrubs		Forbs/ ferns		Grami- noids		Abscissed[a] leaves		Total	
			x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE
Mesic plant communities																
Clearcut/0–10 yrs	6	0.4	1	1	20	5	4	4	24	5	36	8	T[b]	—	85	11
Clearcut/11–20 yrs	6	0.8	16	5	38	10	4	2	14	4	30	6	10	3	112	15
Alnus rubra/21–35 yrs	8	13.2	5	3	10	2	1	T	12	1	23	4	18	5	69	6
Grass-Sedge/21–35 yrs	8	5.1	13	5	15	3	T	T	10	2	53	6	T	T	92	6
Old-growth forest/>200 yrs	4	0.5	2	1	9	1	T	T	15	5	11	4	1	T	38	7
Xeric plant communities																
Clearcut/0–10 yrs	6	1.7	5	5	8	4	4	3	14	3	8	1	0	0	40	7
Clearcut/11–20 yrs	7	4.9	83	23	15	3	16	12	14	3	18	4	2	2	148	27
Unthinned P. menziesii/21–35 yrs	8	37.8	4	2	2	1	26	7	7	1	6	2	T	T	45	9
Thinned P. menziesii/21–35 yrs	8	23.6	11	3	4	1	28	8	4	1	8	1	0	0	55	10
P. menziesii/90–120 yrs	3	0.1	1	1	T	T	45	14	0	T	0	0	0	0	46	15
Old-growth forest/>200 yrs	3	1.3	4	3	1	T	91	10	T	T	0	0	0	0	96	10

[a] Fallen leaves of deciduous shrubs

[b] T < 0.5

Seasonal trends in forage biomass were monitored throughout winter, 1986–1987, within 10, 1 × 1-m quadrats distributed systematically along each of two randomly placed 90-m transects in the following plant communities: 0–10 yr-old clear-cut, 21–35 yr-old *Alnus rubra*, 21–35 yr-old grass-sedge, 21–35 yr-old unthinned *Pseudotsuga menziesii*, and xeric old growth. We estimated cover of herbaceous forages and low evergreen shrubs along those transects in November 1986, and in January, February and April 1987, and subsequently converted cover estimates to biomass estimates using the weight-cover-height regression equations developed in November. Biomass of available deciduous shrubs and ferns was determined in November from average twig counts and weights. Biomass of deciduous shrubs and ferns was estimated again in January, February, and April 1987 by adjusting November estimates of biomass by the ratio of canopy cover measured during winter as a proportion of canopy cover measured during November. The adjustment of November estimates of biomass based on seasonal changes in canopy cover was necessary because twigs were not counted and weighed during winter, and was justified based on general linear relationships existing between shrub biomass and cover (Peek, 1970).

Fecal composition.—Botanical composition of diets was assessed using microhistological identification of fecal forage fragments. Four composite fecal samples were obtained on each winter range within 2 days of 1 November 1986, 15 January, 15 February and 15 April 1987. Composite fecal samples were collected for each of four separate bands of elk encountered in each study area (n = 4 per study area). Composites were compiled from 10 fecal pellets obtained from each of 5–8 individual elk within a band. Fresh fecal pellets were obtained from animals observed defecating, from recently vacated bedsites, or by backtracking observed animals. All samples were stored at −17 C for 1–4 mo, oven-dried at 60 C for 48 h, and were ground through a 1-mm sieve in preparation for analysis.

Fecal composition was determined following the frequency conversion technique described by Sparks and Malechek (1968) and re-evaluated by Holechek and Gross (1982). Frequencies of occurrence of each plant species were determined from 20 microscope fields (125×) viewed on each of 20 slides prepared from each composite fecal sample. The technician conducting these analyses had accumulated over 750 h analyzing elk fecal composition in the Cascade Mountains. Although diet composition determined from fecal analysis may be biased by differential digestibility and fractioning of forage classes (Holechek *et al.*, 1982), we believe the method provided an accurate index of differences in diets between two study areas.

Forage quality.—Dry matter digestibility and crude protein contents were estimated throughout the winter for 22 principal forage species used by elk. A principal forage was defined as any forage species comprising >2% of any seasonal fecal sample. Composite samples of each principal forage species were collected during the weeks centered on 1 November 1986, 15 January, 15 February and 15 April 1987. Composite samples were collected from a minimum of 20 plants throughout the study areas and consisted of plant parts believed to be selected by elk, which in all cases consisted of a fraction of the current year's growth. Plant parts selected were determined by examining adjacent browsed plants. All samples were oven-dried at 40 C within 6 h of clipping, ground through a 1-mm sieve, and stored in air-tight plastic bags at room temperature for 1–5 mo until they were analyzed. Dry matter digestibility was estimated using two-stage in vitro procedures of Tilley and Terry (1963), using inoculum from a fistulated heifer maintained on ryegrass hay and supplemental grain. Crude protein was measured using the micro-Kjeldahl technique (Horowitz, 1980:858). All results were expressed on a 100% dry weight basis.

Indices of diet quality.—Nutritional quality of elk diets was estimated from composition of feces and nutrient content of specific forages. Indices of dietary dry matter digestibility
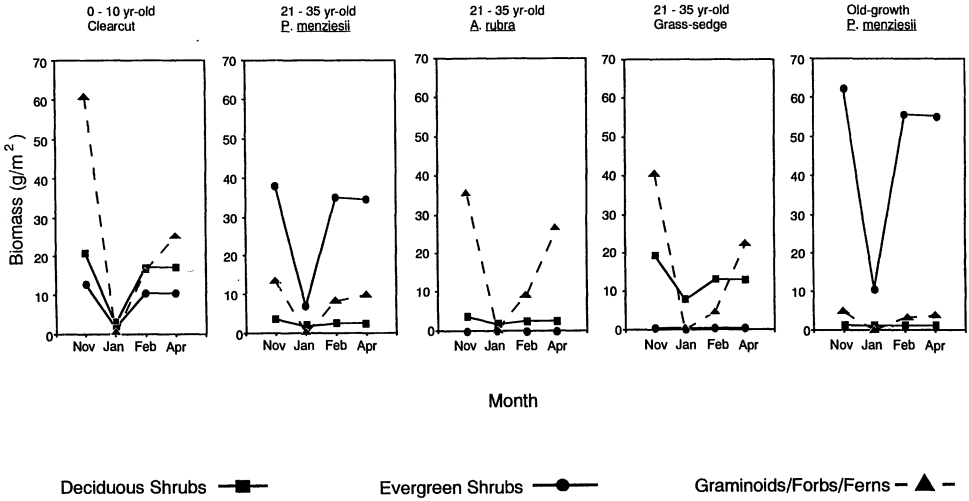
FIG. 1.—Seasonal mean biomass (g/m²) of forage classes available to elk in selected plant communities, November 1986–April 1987

and crude protein were computed as the nutrient value of each forage weighted by its seasonal proportion in the feces. If nutrient data were absent for a forage species, mean levels for the forage class were substituted.

Statistical analysis.—Two-factor analysis of variance was used to determine seasonal and site differences in composition of elk feces and indices of dietary quality. Because we made several simultaneous comparisons of forage class composition of elk feces that were not independent, we elected to control Type I error rates for simultaneous comparisons at $P \leq 0.10$. Hence, for each of five individual comparisons of forage class composition differences were considered significant at $P \leq 0.02$ (*i.e.,* 0.10/5). Differences in in vitro dry matter digestibility and crude protein content were interpreted individually at $P \leq 0.05$. If indices varied among seasons, Fisher's protected LSD test was used to determine significance of all pairwise seasonal comparisons ($P \leq 0.05$).

RESULTS

Forage availability.—Deciduous shrubs, graminoids and forbs/ferns dominated vegetation development in the mesic sere (Table 1). Graminoids and forbs were most prevalent in mesic 0–10 yr-old clear-cuts and in 21–35 yr-old grass-sedge stands. Biomass of available deciduous shrubs was greatest in 11–20 yr-old clear-cuts in mesic bottomlands. Biomass of abscissed leaves, primarily of red alder and black cottonwood (*Populus trichocarpa*), was greatest in 21–35 yr-old *Alnus rubra* communities.

Evergreen shrubs and conifers dominated vegetation development in the xeric sere (Table 1). Biomass of evergreen shrubs increased with age and was greatest in xeric old-growth forests. Biomass of available coniferous browse, primarily Douglas fir, was greatest in 11–20 yr-old xeric clear-cuts, but it diminished when overstories closed over in 21–35 yr-old stands. As in mesic bottomlands, biomass of available deciduous shrubs, forbs and graminoids peaked in early seral stages of xeric plant communities, but at lower levels than in mesic communities.

Seasonal trends in available biomass, measured in selected plant communities, were influenced strongly by snow during January (Fig. 1). Snow virtually eliminated the available herbaceous forage in January; it greatly reduced available evergreen shrubs, but had comparatively less effect on deciduous shrubs. Following snowmelt in February, biomass of available deciduous and evergreen shrubs was comparable to biomass measured in November. Biomass of available herbaceous forages, however, was only 11–27% of that measured in November in open habitats (*e.g.*, grass-sedge, 0–10 yr-old clear-cut, and 21–35 yr-old *Alnus rubra*), and 62–68% of that measured in November in 21–35 yr-old and old-growth conifer stands.

Fecal composition.—Composition of elk feces differed among sampling periods (Table 2). Feces generally contained more forb, graminoid and deciduous shrub material during November than during winter (Table 2, $P < 0.02$). Deciduous shrubs, notably red alder, willow (*Salix* spp.), black cottonwood and huckleberry, were prevalent in autumn feces.

Feces of elk contained more conifers and evergreen shrubs during mid-winter than during November and April (Table 2, $P < 0.02$), particularly during January when snow covered low-lying forages. Important evergreens included Pacific yew (*Taxus brevifolia*), western redcedar (*Thuja plicata*), western hemlock, trailing twinflower and salal. Consumption of evergreens declined during spring green-up in April while that of forbs and grasses increased.

Composition of feces also differed between elk in old-growth and regenerating forests (Table 2). Overall, grasses and forbs were more prevalent in the feces of elk in regenerating than in old-growth forests (Table 2, $P < 0.02$), whereas conifers and evergreen shrubs were more prevalent in feces of elk in old-growth forests (Table 2, $P < 0.02$).

Forage quality.—Forage dry matter digestibility and crude protein content generally decreased between autumn and winter and increased the following spring (Table 3). Nutrient levels of coniferous browse remained relatively constant through autumn, winter and spring, whereas nutrient levels of grasses, forbs and deciduous shrubs increased markedly between midwinter and April. Grasses and forbs had the highest levels of dry matter digestibility and crude protein throughout winter, reflecting low lignin contents and high proportions of cell contents (Cook, 1972). Aquatic forbs, such as water parsley and American veronica (*Veronica americana*), were succulent all winter and provided a limited, yet highly nutritious, winter forage on hydric sites. Evergreen shrubs, conifers and deciduous shrubs, with the exception of trailing blackberry, generally contained low levels of dry matter digestibility and crude protein during winter.

Indices of diet quality.—Indices of diet quality were consistently greater in regenerating forests than in old growth (Fig. 2, $P < 0.05$). Magnitude of the difference varied seasonally (site × season interaction, $P < 0.05$) for both dry matter digestibility and crude protein. Estimated dry matter digestibility and crude protein content of elk diets were lowest during January and February, intermediate during November, and highest during April (Fig. 2, $P < 0.05$). Both indices increased more from February to April in the regenerating forest than in old growth.

DISCUSSION

Succession on xeric alluvial terraces of the White River produced the classic picture of forage development that has emerged from comparable studies in the Pacific Northwest (Irwin and Peek, 1979; Alaback, 1982; Hanley, 1984); *i.e.*, clear-cutting produced a pulse of deciduous shrubs, forbs and graminoids that persisted for approximately 20 yr until they were shaded out by dense overstories or understories dominated by salal. Furthermore, our results corroborated findings that forage successional trends in mesic habitats were less predictably related to age than in xeric uplands (Hanley, 1984). Forbs and graminoids

TABLE 2.—Mean percentages and standard deviations (n = 4) of plant species in feces of elk inhabiting old-growth and 1–35-yr-old regenerating forests, November 1986–April 1987

Species	P-value Mo	P-value Site	Old-growth forest Nov x̄	Nov SD	Jan x̄	Jan SD	Feb x̄	Feb SD	Apr x̄	Apr SD	Regenerating forest Nov x̄	Nov SD	Jan x̄	Jan SD	Feb x̄	Feb SD	Apr x̄	Apr SD
Deciduous shrubs																		
Alnus rubra			10.2	2.2	2.0	1.5	7.9	3.6	4.4	0.8	3.3	1.9	1.0	0.2	3.4	0.8	1.4	1.0
Populus trichocarpa			2.5	2.8	0.5	0.3	0.3	0.2	0.4	0.2	2.2	1.2	0.9	0.5	0.3	0.2	0.8	0.3
Rubus spectabilis			2.3	1.8	0.9	0.4	2.1	0.3	2.2	0.3	1.7	2.0	1.0	0.8	1.8	0.8	3.1	1.1
Rubus ursinus			1.1	0.6	0.7	0.3	0.9	0.1	1.6	1.0	2.4	0.5	1.2	0.8	1.1	0.9	1.4	0.6
Salix spp.			2.5	0.5	1.3	0.7	0.9	0.5	1.5	0.2	10.4	6.1	1.1	0.3	2.1	0.6	3.1	1.4
Vaccinium spp.			5.7	2.0	1.2	0.4	0.6	0.3	1.3	0.7	0.9	0.6	0.5	0.5	0.1	0.0	0.3	0.2
Other[b]	<0.01	0.21	13.7	1.0	11.6	0.7	9.6	1.0	11.6	2.2	12.5	0.8	12.5	2.7	11.1	2.1	9.8	1.4
Totals			38.0	7.5	18.2	2.9	22.3	5.2	23.0	4.3	33.4	6.1	18.2	5.6	19.9	4.1	19.9	1.3
Forbs and ferns																		
Equisetum arvense			0.2	0.1	0.1	0.0	0.1	0.1	0.2	0.1	5.1	2.7	1.9	1.4	1.6	2.3	1.2	0.8
Fragaria spp.			1.3	0.7	0.4	0.2	0.5	0.2	0.7	0.2	1.6	0.8	0.4	0.2	0.4	0.1	2.0	0.9
Hypochaeris radicata			0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.2	0.1	0.1	0.0	0.0	0.5	0.3	2.2	0.4
Oenanthe sarmentosa			0.8	0.8	0.5	0.3	0.4	0.4	0.4	0.4	1.4	0.7	0.7	0.4	1.6	1.6	2.0	1.0
Polystichum munitum			0.7	0.6	1.0	0.7	0.8	0.6	0.6	0.2	0.4	0.2	2.3	1.3	3.7	1.4	0.4	0.3
Trifolium spp.			0.4	0.4	0.4	0.4	0.8	0.8	2.8	0.2	1.8	0.5	0.2	0.1	0.6	0.2	1.8	0.2
Other[c]	<0.01	<0.01	5.2	0.2	4.1	1.0	4.8	0.4	12.5	1.7	15.8	2.0	6.8	1.2	11.0	1.8	16.7	2.2
Totals			8.6	3.1	6.5	2.6	7.4	1.8	18.3	4.2	26.2	3.9	12.3	3.3	19.4	3.3	26.3	4.9
Conifers																		
Pseudotsuga menziesii			0.7	0.2	3.1	1.1	3.9	0.7	6.4	0.6	0.1	0.2	1.5	1.1	2.2	0.6	0.9	0.3
Taxus brevifolia			12.4	4.5	15.5	7.7	9.0	4.0	5.3	1.7	1.0	0.6	11.1	9.3	0.7	0.6	1.0	1.3
Thuja plicata			5.2	1.1	17.7	6.2	13.9	2.9	15.4	5.2	0.7	0.3	6.7	1.2	6.2	3.3	2.8	2.5
Tsuga heterophylla			1.4	0.9	7.2	4.1	4.3	2.2	3.5	2.8	0.8	0.8	2.6	1.9	3.2	1.0	2.5	1.1
Other[d]	<0.01		5.3	0.5	7.3	2.0	3.1	0.7	2.8	0.7	1.5	0.4	3.4	1.1	1.6	0.6	0.3	0.1
Totals			25.0	6.3	50.8	6.0	34.2	5.8	33.4	7.8	4.1	1.0	25.3	12.7	13.7	4.8	7.5	4.4
Evergreen shrubs																		
Arctostaphylos uva-ursi			2.2	0.9	1.1	0.6	0.7	0.3	0.4	0.1	0.7	0.2	0.4	0.1	0.2	0.1	0.1	0.1
Berberis nervosa			0.1	0.1	7.7	8.4	8.7	2.9	3.6	2.8	0.2	0.1	1.0	0.5	0.9	0.5	0.4	0.1
Gaultheria shallon			0.6	0.3	3.4	2.5	2.6	1.0	1.0	0.4	1.5	1.6	4.9	2.4	2.9	0.9	2.5	0.9

TABLE 2.—Continued

Species	P-value[a] Mo	P-value[a] Site	Old-growth forest Nov x̄	Nov SD	Jan x̄	Jan SD	Feb x̄	Feb SD	Apr x̄	Apr SD	Regenerating forest Nov x̄	Nov SD	Jan x̄	Jan SD	Feb x̄	Feb SD	Apr x̄	Apr SD
Linnaea borealis			2.4	2.0	8.7	3.6	13.8	5.9	7.3	0.7	3.4	3.2	10.1	2.9	9.8	1.0	9.9	4.2
Other[c]			1.6	0.3	1.1	0.3	1.8	0.4	0.5	0.2	0.9	0.4	1.1	0.4	0.2	0.1	0.2	0.2
Totals	<0.01	0.03	6.9	2.2	22.0	8.5	27.6	6.9	12.8	3.0	6.7	2.3	17.5	5.4	14.1	2.1	13.0	5.0
Graminoids																		
Agrostis spp.			1.6	1.3	0.2	0.1	0.8	0.4	1.3	0.6	2.1	1.0	1.9	0.6	3.0	1.8	3.1	1.1
Elymus glaucus			1.5	1.0	0.3	0.4	0.3	0.1	0.5	0.4	2.0	1.5	1.7	1.4	0.5	0.5	0.5	0.1
Festuca arundinacea			1.4	0.4	0.3	0.3	0.8	0.2	0.8	0.4	2.0	1.1	2.1	1.1	2.0	0.7	1.9	0.5
Festuca spp.			2.6	1.1	0.4	0.4	1.2	0.8	1.4	1.0	3.0	3.1	2.9	0.7	2.0	0.7	1.7	0.5
Holcus lanata			0.2	0.2	0.0	0.0	0.1	0.1	0.1	0.1	1.7	1.4	2.9	2.7	2.1	1.2	1.2	0.7
Juncus spp.			4.1	3.7	0.1	0.1	1.0	1.0	2.2	0.7	3.0	2.4	4.7	2.1	10.7	2.0	12.2	2.2
Phleum pratense			1.9	1.3	0.4	0.4	1.2	0.9	1.2	0.3	4.6	1.4	2.9	0.4	2.5	1.4	1.8	1.1
Poa spp.			1.4	0.7	0.2	0.2	0.8	0.2	1.2	0.7	1.7	0.9	2.0	0.7	2.6	1.9	2.8	0.6
Other[f]			6.5	0.9	0.8	0.5	2.5	0.6	4.0	0.3	9.1	0.7	5.8	1.0	7.6	1.0	8.3	1.3
Totals	0.02	<0.01	21.2	3.8	2.7	2.7	8.7	3.9	12.7	3.7	29.2	5.0	26.9	7.8	33.0	7.6	33.5	4.3

[a] Probability of the F-ratio for month and site (old growth vs. regenerating forest) main effects. Month × site interaction was insignificant (P > 0.02) for all forage classes.

[b] Shrubs comprising <2% of a seasonal diet include: Acer circinatum, Amelanchier alnifolia, Cornus stolonifera, Lonicera involucrata, Oplopanax horridum, Ribes spp., Rosa spp., Rubus spp., Sambucus racemosa, Spiraea douglasii, and unidentifiable shrubs

[c] Forbs and ferns comprising <2% of a seasonal diet include: Athyrium filix-femina, Anaphalis margaritacea, Blechnum spicant, Circium vulgare, Epilobium spp., Galium spp., Lactuca muralis, Lotus spp., Lupinus spp., Lysichitum americanum, Montia sibirica, Plantago spp., Prunella vulgaris, Ranunculus spp., Smilacina stellata, Stachys cooleyae, Taraxacum officinale, Tiarella trifoliata, Tolmiea menziesii, Veronica americana, V. officinale, Viola spp., unidentifiable ferns, and unidentifiable forbs

[d] Conifers comprising <2% of a seasonal diet include: Abies grandis and unidentifiable conifers

[e] Evergreen shrubs comprising <2% of a seasonal diet include: Chimophila umbellata, Cornus canadensis, Pyrola spp., and unidentifiable evergreen shrubs

[f] Graminoids comprising <2% of a seasonal diet include: Bromus spp., Carex spp., Dactylis glomerata, Deschampsia spp., Lolium perenne, Luzula spp., and unidentifiable grasses

persisted at least 35 yr following logging in mesic sites along the White River, apparently due to combined influences of high water tables and heavy browsing by elk, which impeded development of a forest overstory and favored the persistence of grazing-resistant perennial grasses. We agree with previous conclusions that an abundance of midseral stages of forest regeneration in a landscape would reduce forage values (Wallmo and Schoen, 1980), but we add that local variability in successional patterns on mesic sites may partially mitigate effects of forest succession in uplands.

Winter forage availability was highly variable and influenced strongly by snow cover. By contrast to our study, forages of black-tailed deer on Vancouver Island generally were more available in old-growth forests than in cutover stands due to greater accumulation of snow in cutover forests, greater vertical distribution of browse in old-growth forests (Harestad et al., 1982; Bunnell and Jones, 1984) and greater litterfall of arboreal lichens and conifer boughs in old growth (Stevenson and Rochelle, 1984). Deciduous shrubs and herbaceous forage were more abundant in young seral forests than in old growth in the White River, but evergreen shrubs tended to be more available in old-growth than in regenerating forests, particularly after a snow. We did not measure differences in litterfall among forest seral stages. However, elk feces contained more Pacific yew and western redcedar following a snowfall, both of which appeared more available in old growth than in seral forests either as litterfall or due to the weighing of boughs with snow.

Seasonal and spatial variability in fecal composition broadly reflected differences in available forage. Generally graminoids, forbs and deciduous shrubs were less prevalent in elk feces when they were less accessible following a snowfall than during snowfree periods. Conifers and evergreen shrubs, by contrast, tended to be more prevalent in the feces following a snowfall. Also, herbaceous forages were consumed more by elk in 1–35 yr-old regenerating forests, where mean standing-crop biomass (MSCB) of grasses and forbs averaged 12–63 g dry matter (DM)/m², than in old-growth forests where MSCB averaged 0–26 g DM/m² (Table 1). Consumption of evergreen shrubs, by contrast, was higher in old-growth forests, where MSCB tended to be higher (91 g DM/m²) than in regenerating stands (0–28 g DM/m²).

Elk in 1–35 yr-old regenerating forests of the White River area consumed more herbaceous forages and less shrubs, conifers and evergreen browse than did elk in old-growth forests of Olympic National Park (Leslie et al., 1984) or in managed forests of Vancouver Island (Janz, 1983). Comparable use of herbaceous forage during winter has been reported only in northwestern California and coastal Oregon where herbaceous forages were accessible in meadows and clear-cuts, respectively, and low accumulations of snow permitted access to low-lying herbaceous forages (Harper et al., 1967; Harper, 1985).

In the White River, elk sought abscissed leaves of alder and cottonwood when they were abundant during a brief period of leaf-fall in November (MSCB = 18 g DM/m²), particularly in old growth where grasses were comparatively scarce (Table 1). Leslie et al. (1984) reported similar observations of browsing on fallen leaves by Roosevelt elk in old-growth Sitka spruce (Picea sitchensis)-western hemlock forests, where herbaceous forage was comparably scarce.

Hobbs et al. (1981) concluded that changes in diet selection of elk during winter in the Rocky Mountains were related more to changes in forage quality than to standing crop of vegetation. During a mild winter in the White River, however, as elsewhere in the Pacific Northwest (Leslie et al., 1984; Janz, 1983; Hanley and McKendrick, 1985), many herbaceous forages remained green all winter, particularly in seeps and moist bottomlands, and they provided a digestible source of energy and crude protein throughout winter (Table 3). Winter diet selection of elk in the White River area, therefore, appeared to be more

TABLE 3.—Percentages of in vitro dry-matter digestibility (IVDMD) and crude protein (CP) content in principal elk forages[a]

Species	1 Nov.		15 Jan.–15 Feb.		15 Apr.	
	IVDMD	CP	IVDMD	CP	IVDMD	CP
Deciduous shrubs[b]						
Alnus rubra	32	11	29	8	39	23
Populus trichocarpa	43	4				
Rubus spectabilis	34	6	29	5	43	20
Rubus ursinus	46	8	48	10	50	20
Salix spp.			27	5	42	22
Vaccinium spp.	37	7	37	6	64	13
x̄ (SD)	38 (6)	7 (3)	34 (9)	7 (2)	48 (10)	20 (4)
Forbs and ferns						
Equisetum arvense					60	15
Fragaria virginiana					51	15
Hyochaeris radicata			69	9	79	15
Oenanthe sarmentosa	74	16	67	21	79	24
Polystichum munitum			29	11		
Trifolium spp.	64	16	43	17	68	24
x̄ (SD)	69 (7)	16 (0)	52 (19)	15 (6)	67 (12)	19 (5)
Conifers						
Pseudotsuga menziesii			37	5	33	5
Taxus brevifolia	40	6	39	5	44	5
Thuja plicata	34	7	33	4	40	4
Tsuga heterophylla			35	5	34	5
x̄ (SD)	37 (4)	6 (1)	36 (3)	5 (1)	38 (5)	5 (1)
Evergreen shrubs						
Arctostaphylos uva-ursi	39	5	39	5		
Berberis nervosa			39	6	42	6
Gaultheria shallon	28	5	29	4	32	10
Linnaea borealis	36	6	33	5	47	4
x̄ (SD)	34 (6)	5 (1)	35 (5)	5 (1)	40 (8)	7 (3)
Graminoids						
Juncus spp.			42	7		
Grass[c]	62	12	53	11	78	21

[a] Principal forages comprised >2% of feces

[b] Samples collected in November and April contained leaves and stems, whereas samples collected in January and February contained stem material only

[c] Values are means derived from 4 independent samples of unidentified grass species that were observed eaten by elk

closely related to broad changes in snow accumulation and forage availability than to small changes in forage quality. Overall, our findings confirmed the dietary plasticity of elk reported in the Rocky Mountains (Hobbs *et al.,* 1981), but they suggested that grasses and forbs were preferred forages throughout winter when they were available.

Indices of dietary crude protein content in the White River area (6–9%) were comparable to values previously reported for Roosevelt elk during winter in the Pacific Northwest (7–
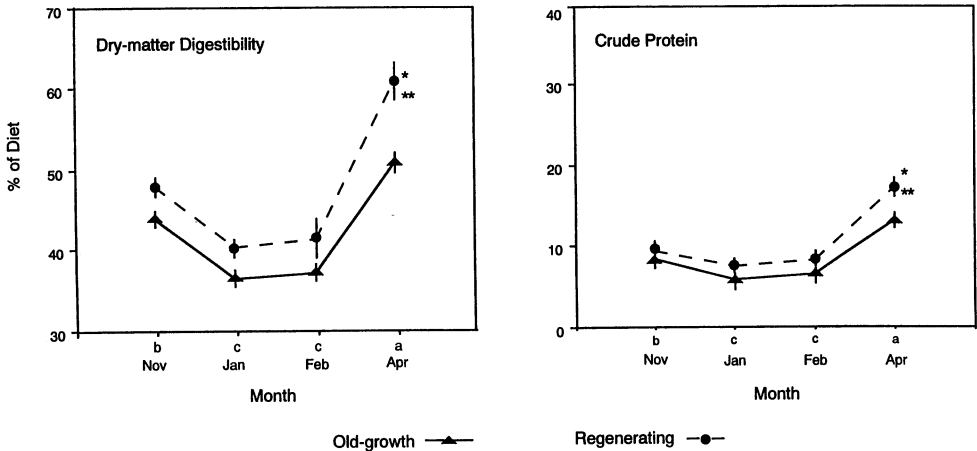
FIG. 2.—Indices of dry matter digestibility and crude protein levels (x% ± SD, n = 4) in seasonal diets of elk inhabiting old-growth and 1–35 yr-old regenerating forests, November 1986–April 1987. Different letters between sampling periods indicate significant temporal differences (Fisher's protected LSD test, P < 0.05). * indicates a significant difference for site main effect and ** indicates a significant site × season interaction (two-factor ANOVA, P < 0.05)

8%, Janz, 1983; 8.3%, Leslie *et al.*, 1984). Winter diets containing 5–7% crude protein content are generally considered adequate for meeting metabolic nitrogen requirements and maintaining proper rumen function in elk (Mould and Robbins, 1981), assuming minimal effects of soluble digestion inhibitors (Robbins *et al.*, 1987). We did not measure tannin concentrations of forages selected by elk, but previous studies revealed that tannin contents of deciduous shrubs generally are higher in early- than in late-seral successional stages (Happe *et al.*, 1990). Consequently, differences in digestible protein of diets between old-growth and regenerating forests cannot be assessed from comparisons of crude protein content alone. Additional research is needed to assess nutritional adequacy of crude protein content in browse-dominated diets of elk in the Pacific Northwest.

Indices of dietary dry matter digestibility in the White River area (36–41%) were generally greater than those reported from nearby coastal regions (31–34%, Janz, 1983; 25%, Leslie *et al.*, 1984). Differences in dry matter digestibility may reflect different inoculum sources used in in vitro digestion trials (Milchunas and Baker, 1982), as well as actual regional differences related to greater consumption of herbaceous forages in the White River area. Minimum dietary requirements for dry matter digestibility are difficult to assess because of variable energy requirements, dry matter passage rates in the rumen, and possible associative effects among forages. However, based upon the carrying capacity model and assumptions presented by Hobbs *et al.* (1982), elk would require a minimum digestibility coefficient of 47% to meet ecological energy requirements measured in the Rocky Mountains. Actual forage digestibility requirements of elk will vary regionally, but the estimate compares favorably with conclusions of Ammann *et al.* (1973:200) that ruminants generally cannot maintain body weight on diets that are much below 50% digestible. Diets of elk from throughout the Pacific Northwest appear to be deficient in digestible energy due to low digestibility of diets; however, elk appeared to have greater opportunity to obtain a nutritionally adequate diet in 1–35 yr-old vs. old-growth forests during a mild winter in the White River.

The relative forage values of old-growth and early-seral regenerating forests remain at the core of contemporary issues regarding management of remaining old-growth forests in the Pacific Northwest. Our results suggested that greater availability of herbaceous forages in 1–35 yr-old than in mature forest ecosystems benefitted elk during a mild winter with minimal snow cover. Evergreen shrubs and coniferous browse, however, were important alternate forages of elk when herbaceous forages were unavailable. Evergreen shrubs were most abundant in xeric old-growth forests, suggesting that old growth may be more important following snowfall. Other unmeasured benefits of old-growth forest communities, including lower snow depths and reduced energy costs during winter, would also provide energetic benefits for elk during snowy winters (Parker *et al.*, 1984).

Because feces composition reflected complex interactions among forest successional stage, forage availability and snowfall, it is clear that responses of elk to postlogging secondary succession will vary regionally in response to prevailing winter conditions. Consequently, the development of management plans aiming to optimize timber and elk habitat values will necessarily need to consider prevailing winter severity and local responses of elk to secondary succession. Forest and wildlife managers concerned with improving elk habitat in commercially managed forests should strive to produce a balance between forages used by elk in mature forests during critical winter periods and forages used in early-seral forests during mild winters. We speculate that rapid conversion of mature forest ecosystems, which produces a disproportionate availability of forages within young seral stands, would likely benefit elk populations during successive mild winters, but may adversely affect populations during periodic severe winters and as early-seral foraging areas succeed to mid-seral successional stages.

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